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Correlations between global and regional measures of invasiveness vary with region size

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Abstract

We aimed to assess the utility of the Global Compendium of Weeds (GCW) as an indicator of plant invasiveness, by relating it to invasiveness at smaller scales. We correlated two global measures of invasiveness for alien plant species taken from the GCW (the total number of references for each species and the number of continental areas they are reported from), against distribution data from 18 regions (countries and continents). To investigate relationships between correlation strength and region size and spatial resolution (size of distribution units), we conducted meta-analyses. Finally, invasiveness measures were correlated against the number of habitats occupied by alien plant species and their median abundance in those habitats, in fine-scale vegetation plots in the Czech Republic and the state of Montana (USA). The

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majority of Spearman's rho coefficients between GCW-derived invasiveness and regional distributions were less than 0.4. Correlation strength was positively related to region size and resolution. Correlations were weaker when the number of habitats occupied by a species, and species abundances within occupied habitats, were considered. We suggest that the use of the GCW as an invasiveness measure is most appropriate for hypotheses posed at coarse, large scales. An exhaustive synthesis of existing regional distributions should provide a more accurate index of the global invasiveness of species.

Keywords
Abundance, alien species distribution, database, exotic plant, global invasiveness, range size

Introduction

Rejmánek (2011) defines invasiveness as 'the degree to which a species is able to reproduce, spread from its place of introduction, and establish in new locations.' However, a clear, useable and repeatable measure of the extent to which species are invasive is still lacking. For plants, many studies employ continuous measures of invasiveness in the introduced range, which involve quantifying species distributions – how widespread species are (Stohlgren et al. 2011). Examples of such data include the number of states (van Kleunen and Johnson 2007, Winter et al. 2010), countries (Lambdon et al. 2008, van Kleunen and Fischer 2009, Winter et al. 2009) or provinces (Castro et al. 2005, Zuloaga et al. 2008) where a species is established, the number of grid cells (Williamson et al. 2009, Pyšek et al. 2011, Speek et al. 2011) or the number of habitats (Pyšek et al. 2012a, b) occupied by a species in particular countries, the number of herbarium records for species (Delisle et al. 2003, Fuentes et al. 2012), or various measures of the rates of spread derived from distribution data (Forcella 1985, Pyšek and Prach 1993, Williamson et al. 2005). These measures correspond well to the process of invasion in the strictest sense, which involves spread – at multiple scales – from initial points of introduction (Richardson et al. 2000, Rejmánek 2011).

A recent aim in invasion biology has been to synthesise across the accumulated wealth of studies, in order to elucidate any general patterns regarding both causes and consequences of invasions, across species and regions (Blackburn et al. 2011, Gurevitch et al. 2011). Building generalisations may be hampered by the often very different definitions and measures of invasiveness employed (Guo 2011, Pyšek 2011). Synthesising efforts may therefore benefit from the use of a general measure of invasiveness, which integrates information on invasion success from multiple regions and at multiple scales. Recent studies have used the Global Compendium of Weeds (GCW, Randall 2002) to obtain such a measure of invasiveness for alien plant species (Pyšek et al. 2009, Jenkins and Keller 2010, Dawson et al. 2011, Dostál et al. 2011). The 2002 version of the GCW includes nearly 300 species lists referring to over 20,000 taxa in various regions of the globe, which cite species as being a 'weed', 'casual alien', 'noxious' or 'environmental weed', and 'naturalised', among other labels (Randall 2002).

Use of the GCW as an indicator of invasion success has not gone without criticism (Richardson and Rejmánek 2004). It was not originally devised for the purpose

of quantifying invasiveness of plant species, and the representation of different regions is not equal, with a bias of more references covering North America and Australia than other continents (Pyšek et al. 2009). This is partly due to well-known geographical biases in the quality of information on invasive species globally (Pyšek et al. 2008, Jeschke et al. 2012), but reporting and survey-effort biases can also occur in regional distribution datasets (Lambdon et al. 2008), which are commonly used to quantify invasiveness despite not being originally intended for this use. Given the interest in using, and value in having a general measure of invasion success for plants, the utility of measures derived from the GCW requires validation against multiple measures that are region-specific.

Here we assess the adequacy of the GCW in providing a general indication of invasiveness, by analysing the strength of correlation between two measures of invasion success derived from the GCW, and regional distribution data for 18 regions varying both in their size (spatial extent) and spatial resolution (i.e., the grain of the distribution units used). Distributions of native plant species have been shown to be more closely correlated when the size (Thompson et al. 1998) and resolution (Hartley et al. 2004) of distributions are more similar. For alien species, we might expect the processes involved which determine invasiveness to be more closely matched to those captured by the GCW, when the region is larger (Pauchard and Shea 2006). Environmental heterogeneity changes across scales (Milne 1991) and larger areas may be more likely to contain habitats and environments allowing a species to establish and invade, which are also found elsewhere globally. Heterogeneity of smaller units nested within larger units means that occurrence in a region does not equate with species occurrence everywhere within the region. Thus, we also assess how the relationship between the GCW and regional distribution data may be scale-dependent. Whilst we do not expect relationships to be 1:1, we do expect there to be variation in how much the relationships deviate from 1:1, and we predict the correlations between the GCW and regional measures will be greater when the region is larger, and the resolution coarser.

We also assess (i) the strength of correlation between GCW-invasiveness measures and the number of habitats species occupied, and (ii) their median abundance in those habitats, derived from fine-scale vegetation-plot data in two regions for which such data are available: the Czech Republic and the state of Montana (USA). At the finest spatial resolution of vegetation plots within habitat types, environmental conditions and exposure to alien plant propagules will be strongly site-dependent. At this scale, the identity and characteristics of individual habitat types may be the most important determinant of invasions (Chytrý et al. 2008a). Thus at the finest spatial scale, we expect there to be little or no relationship between local-scale vegetation plot abundance and global invasiveness. Species' commonness can also be indicated by their level of habitat-specificity, i.e. the number of habitats which species can occur in (Rabinowitz 1981). Widespread species within a region also tend to occupy a greater range of habitats (Pyšek et al. 2009, 2011), so we also expect GCW-derived invasiveness measures to correlate well with the number of habitats occupied by a species.

Methods

Data collection

We obtained regional species-distribution data as regional invasiveness measures, for vascular plants for 18 regions in total, on six continents (Table 1). The regions ranged from countries to whole continents (Table 1). The data were obtained largely from online national databases, floras and published literature (see Table 1). Data for the grid-cell occupancy of species in the Czech Republic were obtained from the working database CzechFlor, held at the Institute of Botany, Academy of Sciences of the Czech Republic, Průhonice. The species included in regional datasets were considered at least to be casual (*sensu* Richardson et al. 2000, Pyšek et al. 2004), naturalised (*sensu* Richardson et al. 2000, Pyšek et al. 2004) or weed/invasive species (Table 1). For Europe, and all European countries, only species introduced after AD 1500 ('neophytes') were included.

The number of alien species per region varied from 221 (China) to 3,682 (North America; Table 1). There was no significant correlation between region area and the number of species included (Spearman's ϱ = -0.117, 95% CI = -0.6376, 0.4615, p = 0.644). Region areas were obtained from atlas sources. For regions with non-grid cell distribution units, atlas sources were also used to calculate the mean average area of distribution unit per region, and these values were used as a measure of resolution (Table 1). The largest region was North America (USA + Canada), which also had the coarsest resolution of distribution; the smallest of the 18 regions was New Jersey (Table 1).

Data on the number of habitats/communities and the median abundances of species within those habitats were obtained from vegetation-plot data for the Czech Republic and Montana. Both datasets used originally included native and alien plant species that were present in each plot; however, we excluded the native species for our purposes and included all aliens for Montana and all neophytes for the Czech Republic. The dataset used for the Czech Republic was from Chytrý et al. (2005); it included a stratified selection of over 20,000 vegetation plots from the Czech National Phytosociological Database (Chytrý and Rafajová 2003: GIVD code EU-CZ-001, Dengler et al. 2011); these plots varied in size according to vegetation type (see Chytrý et al. 2005, for details) and contained species-cover records determined according to the Braun-Blanquet or Domin scale (van der Maarel 1979). These plots were classified into 32 habitat types based upon EUNIS Habitat Classification (Davies and Moss 2003; Chytrý et al. 2005). We calculated three metrics from this dataset: (i) the number of habitats occupied by a species, (ii) the average median cover of species across habitats occupied, and (iii) the maximum median habitat cover (i.e. the habitat with the highest median cover). Median covers per habitat were calculated using vegetation plots where a species was present and average median covers per habitat were calculated across habitats where a species was present. The median cover from the habitat with the highest median cover for a species was used as the maximum median cover. For Montana, data were downloaded from VegBank (http://vegbank.org/vegbank/index.jsp, accessed 03/02/2011; GIVD code NA-US-002; Dengler et al. 2011), which in-

Table 1. The 18 regions included in this study and the data sources for the species distributions per region. Also included is the number of species per region, the region area, the unit of distribution used, and the resolution (area of distribution units, average values given for non-grid cell units).

Region	Data Source	No. of species	Species included are at least:	Area (km²)	Unit of distribution (number of units)	Resolution (km²)
Argentina	Zuloaga et al. (2008)	582	Naturalised	3,744,977	Province (24)	162,825
Australia	AVH Australia Virtual Herbarium (http://chah.gov.au/avh/) Australian Government weeds list (http://www.environment.gov.au/cgi-bin/biodiversity/invasive/weeds/weedspeciesindex.pl?id=701)	416	Invasive ('Weeds')	7,617,930	Point record	NA
Chile	Fuentes et al. (2012)	688	Naturalised	757,725	Province (50)	15,155
China	Weber et al. (2008)	221	Invasive	9,677,012	Province (32)	224,621
Europe	DAISIE (http://www.europe-aliens.org/)	1,238	Naturalised	4,767,682	Country/region (23)	207,291
Czech Republic	CzechFlor Database	918	Casual	78,866	Grid cell (679)	132
Germany	FlorKart (http://www.floraweb.de)	427	Casual	357,021	Grid cell (2995)	ca. 130
Great Britain	British and Irish Flora (Preston et al. 2002)	1,340	Casual	229,848	Grid cell (2886)	100
Ireland	British and Irish Flora (Preston et al. 2002)	521	Casual	84,421	Grid cell (1028)	100
Italy	Celesti-Grapow et al. (2010)	922	Naturalised	301,338	Province (21)	15,066
North America	Kartesz (2011)	3,682	Naturalised	19,811,345	State/Province (66)	303,742
Alabama	Kartesz (2011)	777	Naturalised	135,765	County (67)	1,962
California	Kartesz (2011)	1,359	Naturalised	423,970	County (58)	6,969
Florida	Kartesz (2011)	1,057	Naturalised	170,304	County (67)	2,080
Montana	Kartesz (2011)	534	Naturalised	380,838	County (56)	6,801
New Jersey	Kartesz (2011)	683	Naturalised	22,588	County (21)	915
Pennsylvania	Kartesz (2011)	1,038	Naturalised	119,283	County (66)	1,764
South Africa	Weeds and Invasive plants database (http://www.agis.agric.za/wip/)	286	Invasive	1,221,037	Grid cell (1575)	775

cluded 6,251 vegetation plots (also varying in size depending on vegetation type).The same three metrics were calculated as for the Czech plot data (except 'number of communities' replaced 'number of habitats'). The community data in VegBank followed definitions outlined by the guidelines for describing associations and alliances of the US National Vegetation Classification (Jennings et al. 2009). Species cover in plots was measured as percentage of total area. A total of 175 and 158 species were included in the final datasets for the Czech Republic and Montana, respectively.

The Global Compendium of Weeds is the most comprehensive list of weedy and invasive species to date (Randall 2002), and whilst it is not exhaustive, it is still global in scale, and draws on records from all six inhabited continents, and also oceanic islands. We used the GCW to generate two invasiveness measures for species present in each regional dataset. First, all references to a species were counted. Second, the number of GCW areas was counted (11 in total) within which a species was referenced as occurring. These GCW areas were Africa, Europe, North America, Central America, South America, Australasia, Central Asia, South Asia, Middle East, South-East Asia and Pacific Islands (including Hawai'i; see Table S1 in Appendix for further details; Dawson et al. 2011). Additionally, a number of references included within the GCW only record species as 'introduced', which may not indicate that the species has established, or is invasive. Thus, these two invasiveness measures were recalculated, including only those references explicitly referring to species that were weedy, naturalised or invasive (i.e. species were weeds, noxious or environmental weeds, naturalised, invasive alien/exotic, exotic/alien of ecological/conservation concern; these references are hereafter referred to as 'weed only' references). References exclusively citing weeds of agriculture were not included as 'weed only' references.

Analyses

We used Spearman's rank correlation to assess the association between regional distribution data and GCW invasiveness measures, because (i) we did not expect relationships to be linear and (ii) data were skewed and sometimes included outliers. Whilst Spearman's rank correlation is robust to the presence of outliers compared to the product-moment correlation, it can still be affected by heteroscedasticity, and by outliers when they are large in number (Bin Abdullah 1990). To ensure that estimates of Spearman's rho coefficients were robust, we used a resampling-with-replacement bootstrapping procedure (with 9999 sample replicates) in order to calculate 95% confidence intervals (bias-corrected). Confidence intervals not overlapping zero indicate that the correlation between a regional distribution and GCW invasiveness measure is significantly greater than zero. However, the numbers of species within regions are large, and the precision with which one can estimate a correlation coefficient increases with sample size. Thus, even weak correlations are likely to be estimated accurately and differ significantly from zero. Therefore, the strength of the correlations themselves is of greater relevance to this study than whether or not the correlations differ significantly from zero.

Coefficients and confidence intervals were calculated for correlations between distribution data of each region and one of the two GCW-invasiveness measures: (i) the total number of GCW references, (ii) the number of GCW areas a species was recorded in. This was repeated for (iii) the number of 'weed only' category references, and (iv), the number of GCW areas according to 'weed only' category references. In all cases, to avoid non-independence of GCW-derived invasiveness and regional distribution measures, references in the GCW from the area containing the target region considered were always excluded (see Table S1 for description of GCW areas). For example, for correlations involving the German and European regional distribution data, all references of species from Europe were excluded in the calculation of the GCW measures. Similarly, for the data from China, all references from East Asia were excluded, as were all references from North America, when Canadian provinces and USA states were analysed.

We used the random effects meta-analysis approach outlined by Gurevitch and Hedges (1999) to analyse the relationship between correlation coefficient strength and region area or resolution. A Pearson's rank correlation test of area and resolution (both log transformed) revealed that regional areas and resolution were strongly and significantly correlated (Pearson's R = 0.806, 95% CI = 0.531, 0.927, df = 15, P < 0.0001), and so they were considered individually. Australia was excluded from the analyses involving resolution, as the distribution units for Australia were point records.

First, we transformed Spearman's rho coefficients (ϱ) from the correlations between regional distributions and GCW measures, using Fisher's Z transformation:

$$Z = \frac{1}{2}\ln\left(\frac{1+\rho}{1-\rho}\right)$$

The variance associated with each Z-transformed coefficient was calculated as:

$$var\,(Z) = \frac{1}{n-3}$$

where n equals the sample size. This transformation has the benefit of stabilising the variance of the correlation coefficients, reducing heteroscedasticity. We wanted to analyse these transformed coefficients meta-analytically, and to do so, Gurevitch and Hedges (1999) recommend a random-effects approach, to account for random variation that occurs between effect sizes (transformed coefficients in this study). This requires estimation of not only within-region coefficient variances, but also between-region coefficient variances (Gurevitch and Hedges 1999). To achieve this, we ran a fixed effects linear regression model, with Z-transformed correlation coefficients as the effect sizes, and area or resolution (ln-transformed) as the explanatory variable. The between-region variance in coefficients was then extracted and added to the within-region variances (Gurevitch and Hedges 1999). The inverse of these summed within- and between-region variances was then used as weightings per region in a second linear regression model (the actual meta-analysis). Because of the relatively low sample size (17/18 regions), the second linear regression model was bootstrapped with 999 replicates (where the region coefficients

were randomly sampled with replacement), and bias-corrected 95% confidence intervals were inspected to assess the significance of slopes (confidence intervals containing zero indicate that the relationship between correlation strength and region area/resolution is not significantly different from zero). This meta-analytical procedure was conducted for coefficients with each of the GCW-derived invasiveness measures per region.

One potential reason for correlation strength varying between regions could be due to the fact that smaller regions are more likely to have dissimilar, idiosyncratic sets of species compared to the larger regions. To test this, Spearman's rho correlations were conducted between region size (area) and the proportion of species within a region with zero references from elsewhere outside the target region. A negative correlation with region area would be expected, if smaller regions tend to have more idiosyncratic species not found elsewhere. A bootstrapped, bias-corrected 95% confidence interval (9999 replicates; confidences intervals are hereafter referred to as '95% CI') was used to assess significance of the correlation, as above.

For the vegetation-plot data from the Czech Republic and Montana, the same analytical procedure was used as for the individual regional-scale distribution correlations with GCW invasiveness measures. All analyses were conducted using R 2.14.0 (R Development Core Team 2011).

Results

How strongly correlated are GCW invasiveness measures and regional alien plant distributions?

When all GCW references were considered, the correlation between the number of GCW references and regional distribution measures was significantly different from zero for all regions except Germany (Fig. 1). Spearman's rho coefficients ranged from 0.091 (Germany) to 0.523 (California). Despite the significance of the correlations, all of them were far from a 1:1 relationship. Only one region (California) had a correlation strength above 0.5 with this GCW invasiveness measure; the majority of regions (13) had correlation coefficients <0.4 (Fig. 1). When the number of GCW areas recording a species was used as the GCW invasiveness measure, the majority of regions (14) had correlation coefficients slightly (but not significantly) lower than when the number of references was used (Fig. 1). When 'weed only' category references were considered, the correlations between the number of GCW references or GCW areas and regional distributions were similar in strength overall to those obtained when all references were considered (Fig. S2). Correlation strength was also high (>0.4) for North America and Australia (Fig. 1), which are the two regions most over-represented by references in the GCW, suggesting that the GCW is a reasonable correlate of regional alien plant distribution independently of the reference bias for these two regions. The proportion of species per region with zero references outside the target region was not significantly correlated with region area (ϱ=0.170; bootstrapped, bias-corrected 95% CI= -0.4137, 0.6390).

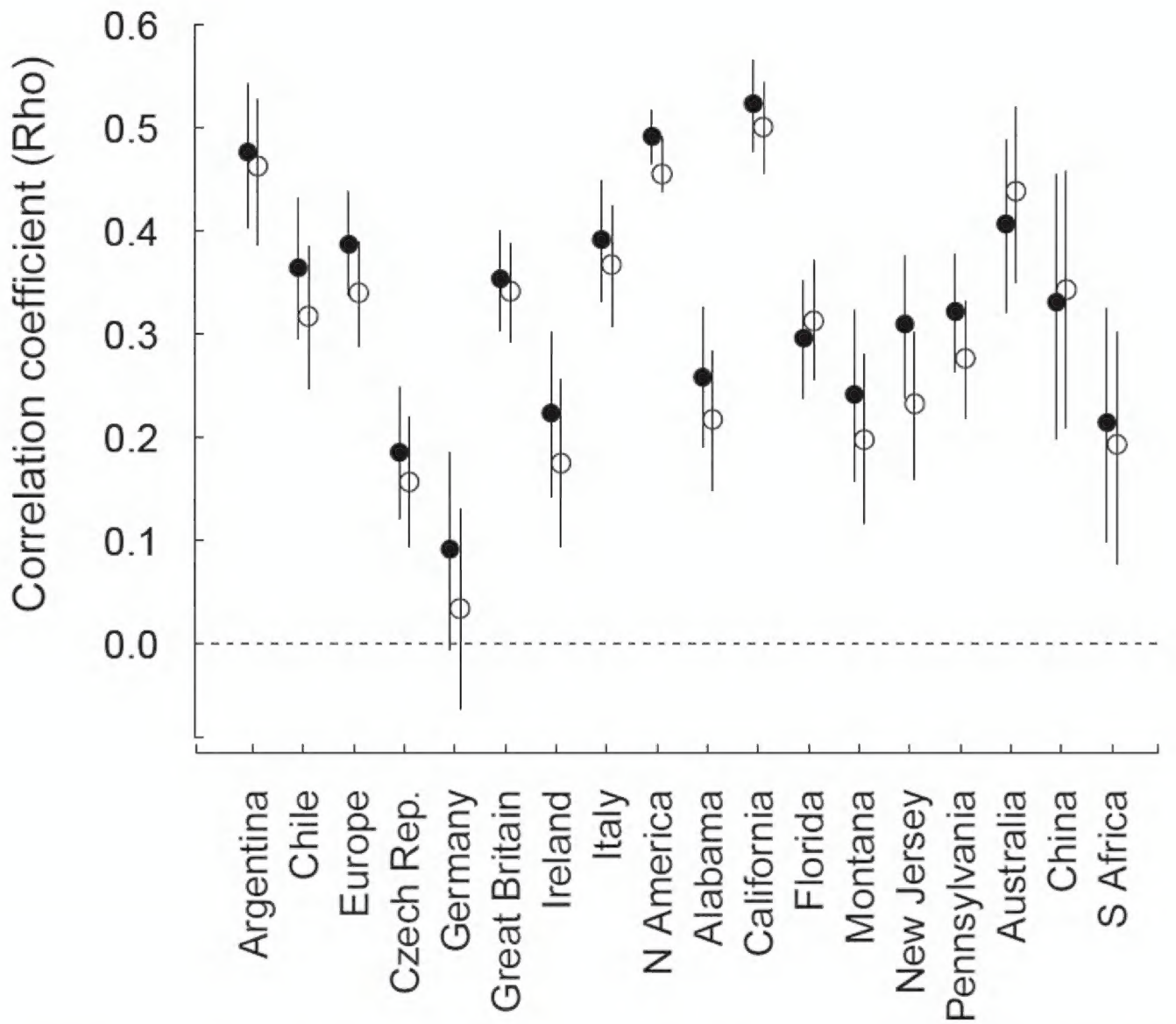

Figure 1. Spearman's ϱ correlation coefficients of the relationship between the number of GCW references (closed circles), or the number of GCW areas occupied (open circles) and the distribution (number of units occupied) of species in 18 regions. GCW measures were calculated using all non-target region references (See Fig. S2 for coefficients using 'weed-only' references). Error bars indicate bootstrapped, bias-corrected 95% confidence intervals; the dashed line signifies ϱ=0.

Is correlation strength related to region area and resolution?

In the meta-analyses, the strength of correlation between GCW-derived invasiveness and regional distributions was significantly and positively related to the area of the target region (Fig. 2a), when the number of references was considered ($\beta_{ln(area)}$=0.035, 95% CI= 0.012, 0.054). A similar significant, positive relationship with area was observed for the number of GCW areas occupied ($\beta_{ln(area)}$=0.041, 95% CI= 0.023, 0.059; Fig. 2a).

The strength of correlation between regional distribution and GCW invasiveness was also related to resolution of distribution units; correlation strength increased with increasing average area of distribution units (Fig.2b). The relationship between resolution and correlation strength was similar whether the number of references ($\beta_{ln(resolution)}$=0.032, 95% CI= 0.015, 0.048) or the number of GCW areas was used ($\beta_{ln(resolution)}$=0.033, 95% CI= 0.013, 0.049; Fig 2b). The relationships between area or resolution and correlation strength were similar when 'weed only' references were used, but less variation in coefficient strength was explained by area, than when all references were used (Fig. S3).

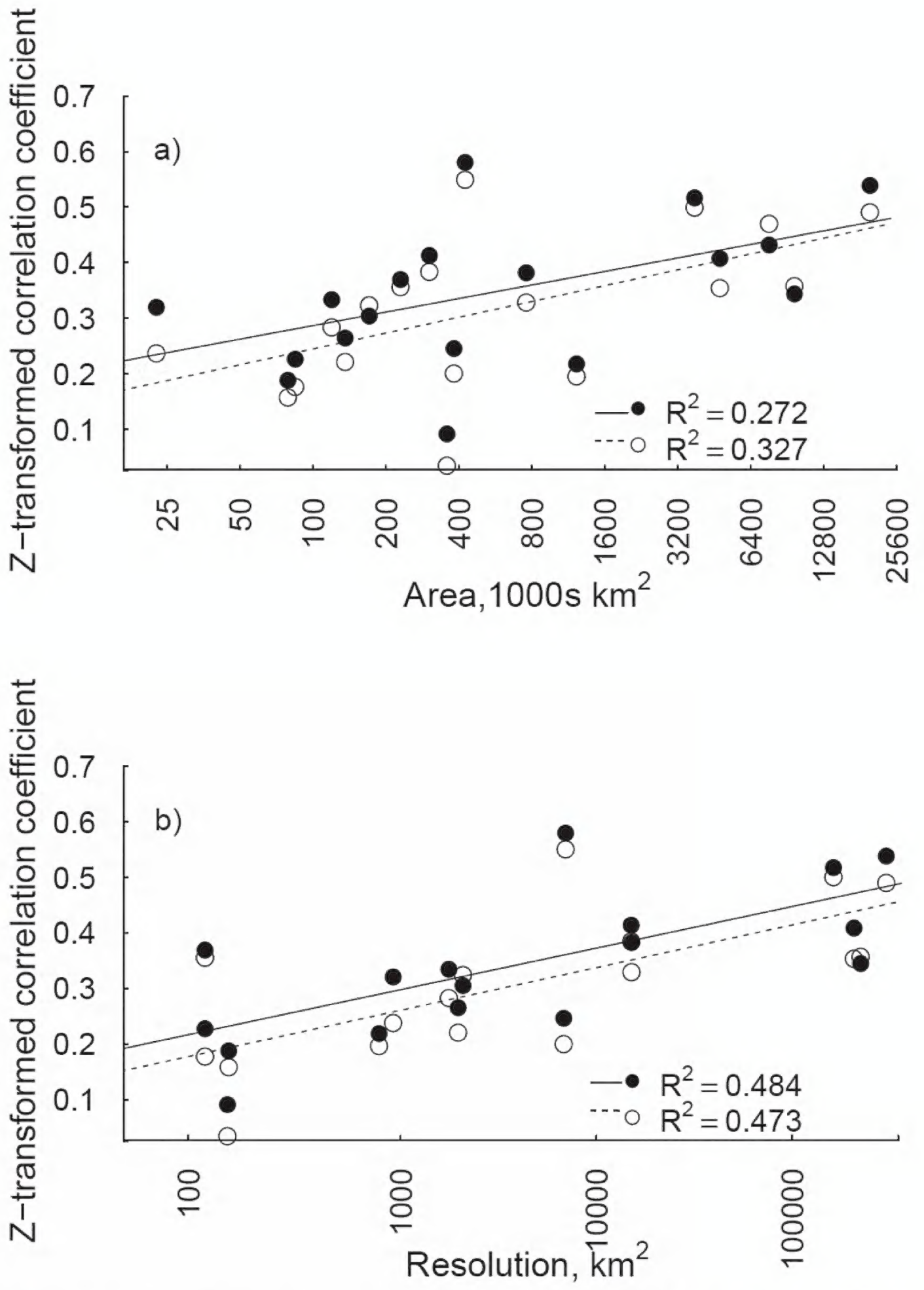

Figure 2. Relationships between the correlation strength (Z-transformed Spearman's ϱ coefficient) of GCW-derived invasiveness measures and regional distributions, and region area (a) and resolution (area of distribution units; b). Solid lines and circles represent the fitted models and correlation strengths per region, respectively, with number of references in the global compendium of weeds as the GCW-invasiveness measure. Dashed lines and open circles are fitted models and region correlation strengths, respectively, with the number of GCW areas as the invasiveness measure. Note the natural log scale on the x axes.

Is invasiveness according to the GCW correlated with number of habitats and abundance at the vegetation-plot scale?

In the Czech Republic, the number of habitats occupied by a species was significantly correlated with GCW invasiveness measures, and the correlation was strongest when number of 'weed only' references was used; however, none of the coefficients were >0.3 (Table 2, Table S4). In comparison, correlation strength for the same set of species was always greater (although not significantly) when the number of occupied 11 × 12 km grid cells in the Czech Republic was considered (Table 2). Maximum median cover in a habitat was not significantly correlated with the number of references or the number of GCW areas occupied (Table 2). Results were similar when 'weed only' references were used, except average median cover in a habitat for the Czech Republic was significantly and negatively correlated (ϱ= -0.15) with the number of GCW areas recording a species (Table S4).

In Montana, the number of plant communities occupied by a species was significantly correlated with the number of GCW references and the number of GCW areas (Table 2). The correlation coefficients for the same set of species were not significant when the number of Montana counties occupied was considered (Table 2). Average median cover in a community was not significantly correlated with the number of

Table 2. Spearman's ϱ correlation coefficients (and bootstrapped, bias-corrected 95% confidence intervals) of relationships between GCW-derived invasiveness measures and regional measures of species abundance and distribution from vegetation-plot data in the Czech Republic and Montana. Also given, for comparison, are correlations for the number of Czech Republic grid cells and the number of counties in Montana occupied by a species, using the subset of species occurring in the vegetation plot data for the respective regions. The values in bold are ϱ coefficients, that are significantly greater than zero. GCW measures included number of references and the number of global regions according to the Global Compendium of Weeds with all non-target region references included.

	GCW invasiveness	
	References	**Areas**
Czech Republic		
Grid-cell data		
Number of 11 km × 12 km squares	**0.382 (0.241, 0.508)**	**0.261 (0.111, 0.400)**
Vegetation plot data		
Number of habitats	**0.282 (0.143, 0.414)**	**0.216 (0.070, 0.349)**
Average median cover per habitat	-0.031 (-0.181, 0.113)	-0.093 (-0.232, 0.053)
Maximum median cover in a habitat	0.072 (-0.080, 0.214)	-0.003 (-0.150, 0.139)
Montana		
County data		
Number of counties	0.168 (-0.023, 0.339)	0.135 (-0.043, 0.309)
Vegetation plot data		
Number of communities	**0.240 (0.057, 0.403)**	**0.223 (0.048, 0.384)**
Average median cover per community	0.114 (-0.049, 0.270)	0.083 (-0.080, 0.241)
Maximum median cover in a community	0.160 (-0.006, 0.315)	0.120 (-0.051, 0.281)

GCW references or the number of GCW areas (Table 2). The maximum median cover of species in a habitat for Montana was significantly and positively correlated (ϱ= 0.19) with the number of 'weed only' references (Table S4).

Discussion

Synthesis of information on plant invasions and risk assessment schemes across multiple studies and regions could benefit from the development of a globally applicable measure of invasion success. We have shown that the correlations between regional measures of invasiveness and measures derived from the Global Compendium of Weeds (Randall 2002) were largely significantly different from zero, but also diverged considerably from a 1:1 relationship. Correlations were stronger for larger, continental-scale regions with coarse resolution, but weaker for smaller areas with finer-scale distribution data.

The weaker correlation between the GCW and fine-scale regional distributions may reflect the incongruence in spatial distribution between scales observed elsewhere for native species (Thompson et al. 1998, Hartley et al. 2004). A shift in the dominant processes affecting species distributions may occur as one moves from fine-scale to coarse-scale distributions (Hartley et al. 2004, Pauchard and Shea 2006). Globally invasive species may have been widely introduced, but at a smaller regional scale they may not be able to establish and spread because of abiotic and biotic environmental barriers, or introduction effort in the region has not been sufficient to allow escape from cultivation. For a larger, continental-scale region, it is more likely that an invasive species will be introduced in sufficient numbers and locations, and encounter favourable conditions somewhere within the region, for establishment and spread to occur. Conversely, some species may be invasive within regions at a local scale, but may not be widespread at a larger, or even global scale due to dispersal restrictions (natural or human), or spatially restricted introduction effort. Just as with rarity in native plants (Rabinowitz 1981), an alien plant that is widespread at a coarse spatial scale can be abundant or rare in many locations throughout the range, or it can be abundant or rare in few but widely distributed locations. Thus, the coarse-scale GCW measure of invasiveness is unable to capture the more complex, fine-scale spatial structure of species distributions, but is more likely to reflect frequency of occurrence of species in larger regions with coarse distribution units. Dissimilarity in species introductions among regions is also likely to increase as the areas of the target regions decrease, leading to poorer correlations between the GCW and region measures. For example, Lloret et al. (2004) found that only one tenth of alien species on eight Mediterranean islands were found on half or more of the islands, indicating a high level of idiosyncrasy in species pools at the local (island) scale. Additionally, Chytrý et al. (2008b) showed that only few neophyte species were shared among the species present within habitats of three separate regions of Europe (see also Stohlgren et al. 2011). However, we found that smaller regions in our study did not have a greater proportion of alien species without references of being alien elsewhere outside the target region, compared to larger

regions. This, coupled with the lack of a correlation between species sample size and region size, suggests that smaller regions are not necessarily more likely to have species pools that are less representative of the global pool than larger regions.

Many of the regions considered in our study are recipients of largely European plant species (Pyšek 1998, Ugarte et al. 2010; Winter et al. 2010, Stohlgren et al. 2011, Fuentes et al. 2012). As most non-European regions considered are larger in area and coarser in distribution resolution than European regions, the relationship between global-regional correlation strength and area/resolution could be an artefact of dissimilarity in introduced species pools. However, this seems unlikely, as the GCW-regional correlation strength for the whole of Europe was still high and similar to that of North America when 'weed only' references were considered. Thus, it seems unlikely that differences in the character of the regional species pools are confounding the effects of area and resolution on GCW-regional correlation strengths. One final potential cause of the poor correlation between the GCW and regional distributions is that many neophyte species have not yet reached their full extent in invaded regions (Williamson et al. 2009, Gassó et al. 2010, 2012). Over time, species may 'fill in' more fine-scale spatial units in a region, potentially reducing the disparity between fine- and coarse-scale distributions.

GCW-derived measures of invasion success were poor correlates of species' abundance in habitats and communities within which they occur. However, the correlations between habitat breadth and GCW invasiveness measures were significant (Table 2). A relationship between range size and habitat breadth was recently reported for the Czech Republic, where the range of habitats occupied by an alien species increased with larger distribution of the species in this country (Pyšek et al. 2011). Species' range sizes may be large, either because of wide niche breadths or because they utilise a widespread resource (Thompson et al. 1998). The results of our study corroborate those of Pyšek et al. (2009) and Dostál et al. (2011), who showed that the likelihood of Central European plant species being introduced and becoming a weed in other regions globally was greater for species with a larger native range size and niche breadth, respectively. However, this does not mean that commonness of those habitats is unimportant. Chytrý et al. (2005) demonstrated that only 6% of neophyte species in the Czech Republic occurred in more than 10 habitat types, and that the highest species richness of neophyte species was in anthropogenic habitats, which are likely to be more common than those relatively undisturbed that are also rarely invaded. Separating out the roles of habitat niche breadth and commonness of optimal habitat type in determining larger scale alien plant distributions thus remains an interesting challenge.

The significant relationship between the number of habitats/communities containing a species and the GCW could potentially be created by a bias toward inclusion of already widespread and established plant species. For example, alien plant species in the Czech vegetation data may not be representative of the entire Czech neophyte flora, as many rare casual aliens will not have been recorded in vegetation plots (Chytrý et al. 2005). This would focus the data on those species clearly able to establish and spread in the region, whilst species not found in vegetation plots could be either widespread or restricted in their global invasiveness. The 347 species in only one grid cell

for the whole Czech neophyte flora had a range of 0 to 62 references in the GCW. In contrast, the subset of 16 species recorded in only one grid cell and also present in the vegetation dataset had a range of 0 to 30 references in the GCW. This may explain why the correlation strength between the GCW and the number of grid cells occupied by species for the Czech vegetation subset was slightly greater than for the entire list of Czech alien species (Table 2; Fig. 1).

Conclusion

There is a need for a general measure of how invasive alien plant species are across different scales, which will facilitate synthesis of existing and on-going studies in invasion ecology. Whilst a general measure of invasion success based upon the Global Compendium of Weeds may be a good starting point as a correlate of coarse-scale distributions of alien plants in larger regions, it is unable to capture more detailed, fine-scale distributions and species abundances at a local scale. If understanding global-scale patterns of invasiveness remains an important goal in this field, efforts should be made to integrate existing distribution data in a more sophisticated manner than simply compiling lists, using common units of distribution in order to capture how widespread alien plant species are and to allow comparisons among species. In the meantime, we recommend that ecologists use the GCW with caution, as a general indicator of invasiveness limited to larger-scale questions.

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Appendix

Table S1. Description of GCW areas used as as measure of invasiveness, based on references in the Global Compendium of Weeds recording a species in a particular global area. The number of references in the Global Compendium of Weeds referring to each global area is listed, along with the countries (or regions) covered.

Areas	Countries/regions covered	Number of references
Africa	East Africa, Egypt, Ethiopia, South Africa, Sudan, Tropical Africa, West Africa, Zimbabwe and Zambia	21
Asia, North and East	Asia (whole), China, Japan, Mongolia, Nepal, Taiwan	15
Asia, South	Bangladesh, India, Pakistan, Sri Lanka	4
Asia, South East	Indonesia, Java (Indonesia), Papua New Guinea, South East Asia (whole), Thailand, Vietnam.	11
Asia, Middle East	Iran and Iraq, Israel, Middle East (whole), Syria	4
Australasia	Australia, New Zealand	52
Central America	Central America (whole), Cuba, Guadeloupe, Jamaica, Mexico, Puerto Rico	10
Europe	Eastern Europe, Europe (whole), Finland, Italy, Mediterranean, Portugal, UK, Western Europe	14
North America	Canada, North America (whole), USA	88
Pacific	Galapagos, Hawai'i, Micronesia, Pacific (whole), Pohnpei	8
South America	Argentina, Brazil, Chile, Guyana, Suriname and French Guiana, Peru, Peru and Ecuador, South America (whole)	16

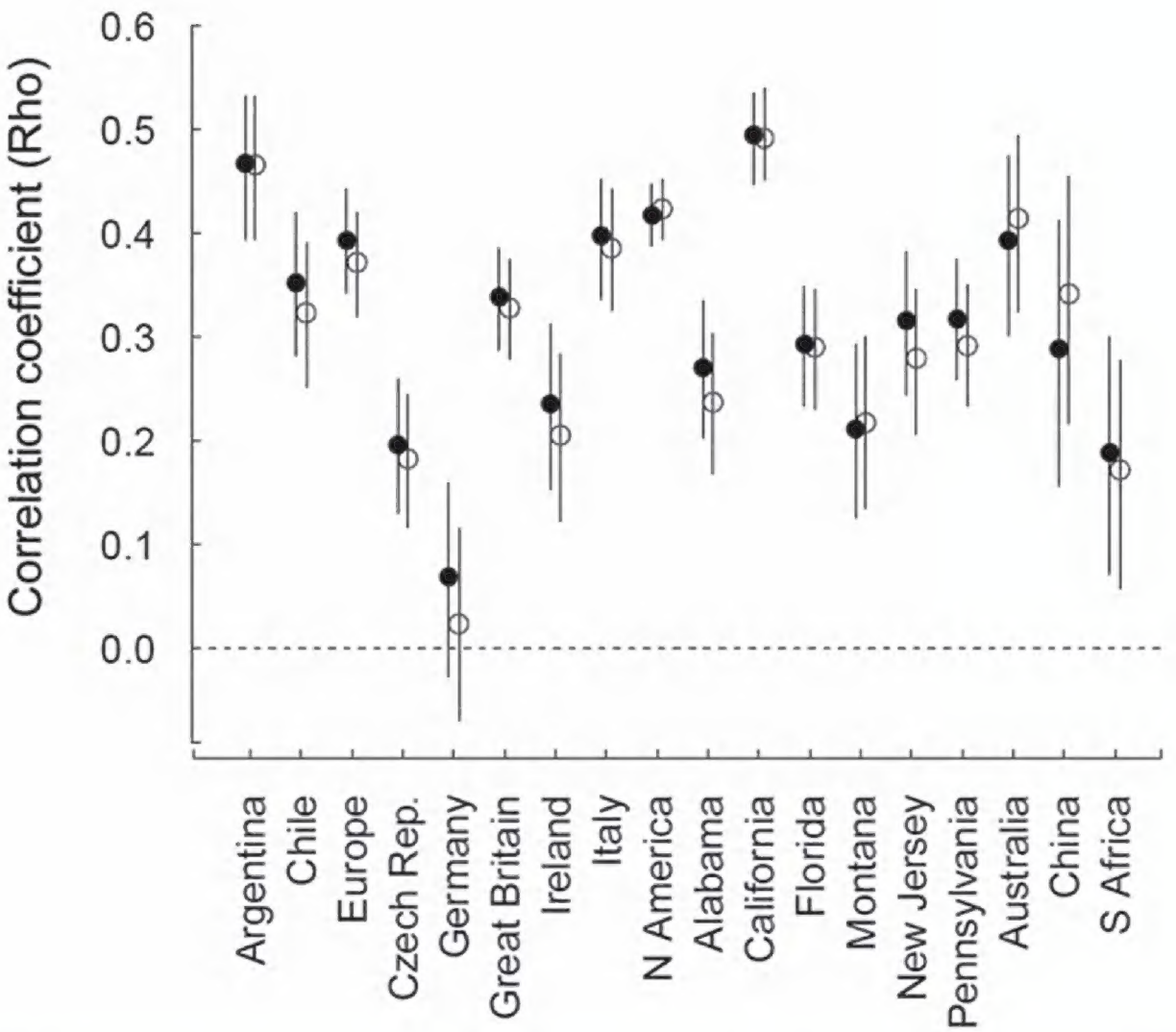

Figure S2. Spearman's ϱ correlation coefficients of the relationship between the number of references in (closed circles), or the number of GCW areas occupied (open circles) according to the Global Compendium of Weeds (using 'weed only' references), and the distribution (number of units occupied) of species in 18 regions. GCW-invasiveness measures were calculated using all non-target region references. Error bars indicate bootstrapped, bias-corrected 95% confidence intervals; the dashed line signifies ϱ=0.

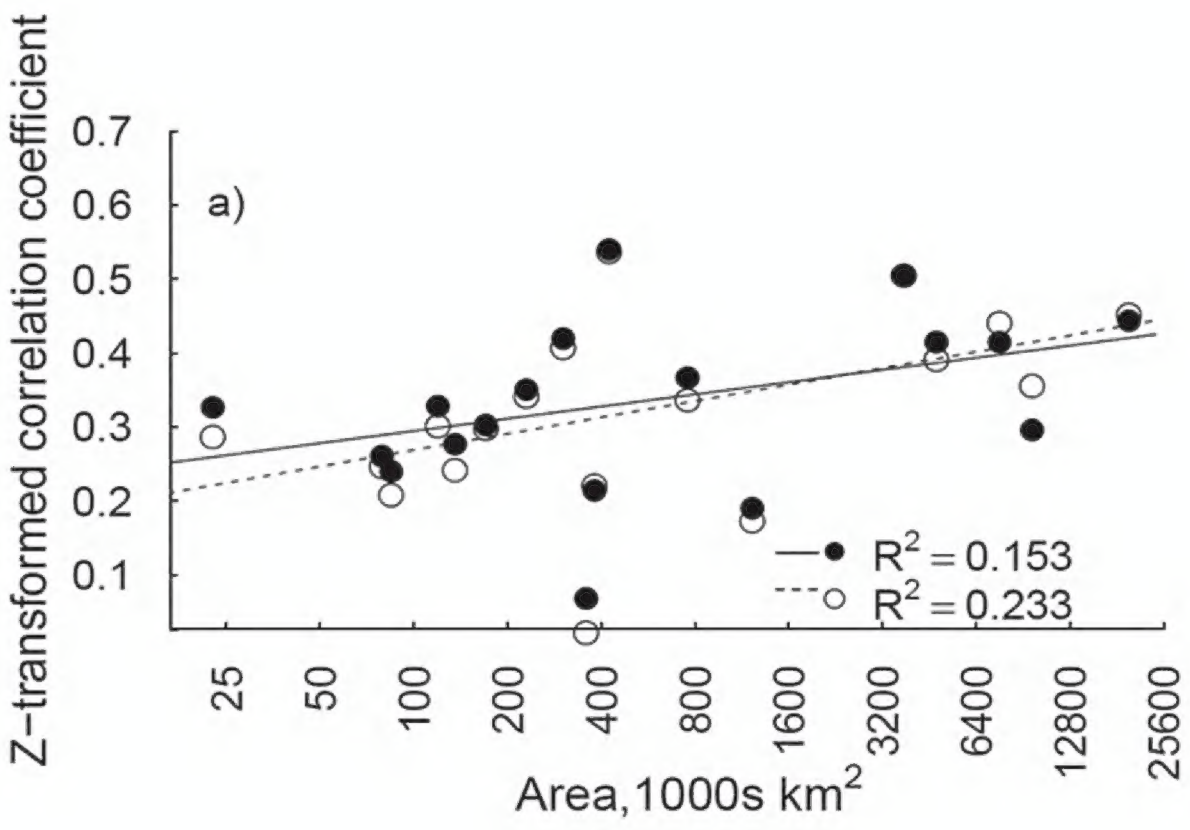

Figure S3. Relationships between the correlation strength (Z-transformed Spearman's ϱ coefficient) of GCW-derived invasiveness measures (using 'weed only references in the Global Compendium of Weeds) versus regional distributions, and region area (**a**) and resolution (area of distribution units; **b**). Solid lines and circles represent the fitted models and correlation strengths per region, respectively, with number of references in the global compendium of weeds as the GCW-invasiveness measure. Dashed lines and open circles are fitted models and region correlation strengths, respectively, with the number of GCW areas as the invasiveness measure. Note the natural log scale on the x axes.

Table S4. Spearman's ϱ correlation coefficients (and bootstrapped, bias-corrected 95% confidence intervals) of relationships between GCW-derived invasiveness measures with 'weed-only' non-target region references included, and regional measures of species abundance and distribution from vegetation plot data in the Czech Republic and Montana. Values in bold are ϱ coefficients significantly greater than zero. GCW measures included number of references and the number of areas occupied according to 'weed only' references in the Global Compendium of Weeds.

	'Weed only' references	
	References	**Areas**
Czech Republic		
Grid cell data		
Number of 11 km × 12 km squares	**0.416 (0.272, 0.542)**	**0.354 (0.204, 0.487)**
Vegetation plot data		
Number of habitats	**0.300 (0.162, 0.431)**	**0.263 (0.117, 0.396)**
Average median cover per habitat	-0.069 (-0.206, 0.079)	**-0.154 (-0.290, -0.005)**
Maximum median cover in a habitat	0.050 (-0.095, 0.193)	-0.043 (-0.187, 0.105)
Montana		
County data		
Number of counties	0.108 (-0.072, 0.291)	0.157 (-0.031, 0.335)
Vegetation plot data		
Number of communities	**0.207 (0.022, 0.375)**	**0.232 (0.049, 0.397)**
Average median cover per community	0.149 (-0.014, 0.304)	0.094 (-0.064, 0.248)
Maximum median cover in a community	**0.189 (0.023, 0.339)**	0.130 (-0.037, 0.285)